

BITING MIDGES FROM DOMINICAN AMBER. I. A NEW FOSSIL SPECIES OF *BAEODASYMYIA* (DIPTERA: CERATOPOGONIDAE)

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Abstract. — *Baeodasymyia dominicana*, a new fossil species of biting midge from Dominican amber is described and illustrated. This is the first fossil species of *Baeodasymyia*, a Neotropical genus with one described extant species known from Colombia and Haiti. *Baeodasymyia* and *Baeohelea* are regarded as sister groups and evidence is presented for the monophyly of each genus. *Baeohelea nana* is recorded for the first time from the island of St. Kitts.

Key Words: Diptera, Ceratopogonidae, biting midges, Dominican amber, fossil species, Neotropical

Fossil Ceratopogonidae are known from sedimentary rocks and amber from many localities in the northern hemisphere, *sensu* Laurasia (Szadziewski 1988, 1990, 1993, Grogan and Szadziewski 1988, Szadziewski and Schlüter 1992). They are relatively common in Cretaceous and Tertiary amber, and the excellent preservation of some specimens allows for as detailed an examination as for extant species. More than 170 fossil species of ceratopogonids have been described to date and several studies are in progress. For example, Borkent (pers. comm.) has completed a manuscript dealing with the ceratopogonid fauna of Upper Cretaceous Canadian amber.

Biting midges from the Tertiary of North America (*sensu* Laurentia) are poorly known. The only described specimens are from Miocene calcareous nodules from California (Palmer 1957, Pierce 1966), but these have little taxonomic value at the present time because most were described from pupae which are poorly known in the extant fauna. Several authors have reported cera-

topogonids from Dominican amber (Schlee and Glöckner 1978, Baroni Urbani and Saunders 1980, Davis 1989). Schlee (1980) found *Heteromyia* sp., and de Melette (1984) found other ceratopogonids in copula in Dominican amber. Undetermined ceratopogonids are known from Mexican amber (Hurd et al. 1962), and we plan on addressing these in a future paper.

Dominican amber occurs in the northern and eastern portions of the island of Hispaniola (Fraquet 1987), and ranges from Upper Eocene to Lower Miocene (Poinar 1990). It has a minimum age of 15–17 million years (Ma) and maximum age of 30–40 Ma (Lambert et al. 1985). Mexican amber from the state of Chiapas, ranges from Upper Oligocene to Lower Miocene and was deposited 22.5–26 Ma (Berggren and Van Couvering 1974).

Both Dominican and Mexican amber probably originated from resins of leguminous trees of the genus *Hymenaea*, especially *H. protera* Poinar (1991). Trees of this genus are now widely distributed through-

Table 1. Families and numbers of Nematocera enclosed in Dominican amber in the collection of the U.S. National Museum of Natural History, Washington (USNM).

Family	No. of specimens	% of total
1. Cecidomyiidae	979	34.94
2. Ceratopogonidae	339	12.10
3. Sciaridae	322	11.49
4. Scatopsidae	279	9.96
5. Psychodidae	277	9.89
6. Chironomidae	274	9.78
7. Mycetophilidae	259	9.24
8. Anisopodidae	33	1.18
9. Culicidae	18	0.64
10. Tipulidae	17	0.61
11. Bibionidae	5	0.18
Total	2802	

out the Greater Antilles and the rest of the Neotropical Region (Grimaldi 1987, Langenheim 1990). This amber formed during a geologic period when Hispaniola, as part of the Caribbean plate, continued on its eastward movement toward its present position (Donnelly 1988), but before the formation of the Isthmus of Panama (Thenius 1977).

Biting midges are common in Dominican amber, representing 12% of the Nematocera in the amber material of the U.S. National Museum of Natural History (Table 1), as opposed to 7–11% of the Nematocera in various Baltic amber collections (Szadziewski 1988). Our goal is to produce a series of papers that describe the ceratopogonid fauna preserved in Dominican amber (Table 2), and attempt to interpret their relationships to the extant New World fauna and the Tertiary fauna of Europe.

MATERIAL AND METHODS

Our studies are based on the examination of 584 ceratopogonids in Dominican amber (Table 2) from the following collections (abbreviations follow those of Arnett and Samuelson 1986): American Museum of Natural History, New York (AMNH); Florida

State Collection of Arthropods, Gainesville (FSCA); U.S. National Museum of Natural History, Washington (USNM); R. Szadziewski personal collection, Department of Invertebrate Zoology, University of Gdansk, Poland (RYSC); Staatliches Museum für Naturkunde, Stuttgart (SMNS).

Specimens were prepared for study in the manner described by Szadziewski (1988). When possible, Canada balsam was used to fill empty cavities in the amber or the insect's body. This allowed detailed examination (to 240×) of male genitalia, antennal sensilla and other structures that otherwise would not have been visible.

Ceratopogonids preserved in Tertiary Baltic, Saxonian or Sakhalin amber are uniformly dark brown, without patterns on their bodies or wings. Baltic and Saxonian amber are considered to be succinites because they contain 3–8% succinic acids (Kosmowska-Ceranowicz and Krumbiegel 1990, Fraquet 1987). Szadziewski (1988, 1990) suggested that loss of color was due to carbonization or some other chemical activity. We now believe it likely that succinic, or other acids, may be partially or totally responsible for such color changes. Because colors are well preserved in biting midges from Dominican and Mexican amber, they probably lack or contain only trace amounts of acids.

Explanations of morphological structures and abbreviations follow those of Downes and Wirth (1981), Szadziewski (1988), and Wirth and Grogan (1988).

Genus *Baeodasymyia* Clastrier and Raccurt

Baeodasymyia Clastrier and Raccurt, 1979:
100. Type-species *Baeodasymyia modesta* Clastrier and Raccurt, by monotypy.

Baeodasymyia dominicana Szadziewski and Grogan, NEW SPECIES Figs. 1–11

Diagnosis.—Distinguished by the following combination of characters: males with 11 antennal flagellomeres, flagellomeres 2–

Table 2. Genera and numbers of Ceratopogonidae enclosed in Dominican amber (see text for names of collections abbreviated).

Genus	Collection					Total	% of total
	USNM	AMNH	FSCA	RYSC	SMNS		
1. <i>Forcipomyia</i>	137	61	41	15	—	254	43.49
2. <i>Brachypogon</i>	140	66	17	1	—	224	38.36
3. <i>Dasyhelea</i>	37	9	7	—	—	53	9.08
4. <i>Culicoides</i>	9	17	3	—	—	29	4.97
5. <i>Stilobezzia</i>	5	2	2	1	—	10	1.71
6. <i>Atrichopogon</i>	8	—	—	—	—	8	1.37
7. <i>Baeodasyomyia</i>	1	1	—	—	—	2	0.34
8. <i>Nannohelea</i>	1	—	—	—	—	1	0.17
9. <i>Heteromyia</i>	—	—	—	—	1	1	0.17
10. <i>Palpomyia</i>	1	—	—	—	—	1	0.17
11. <i>Phaenobezzia</i>	—	1	—	—	—	1	0.17
Total	339	157	70	17	1	584	

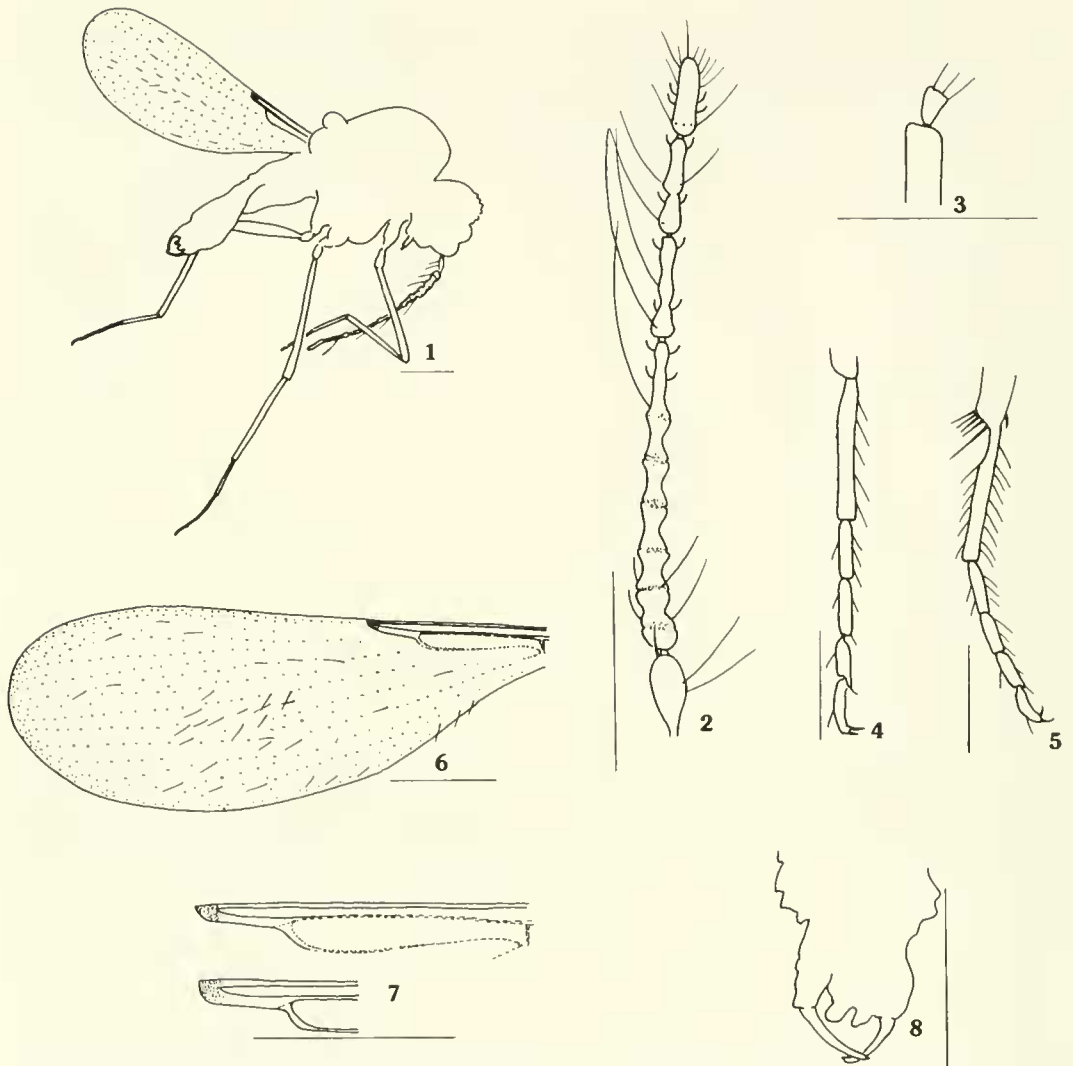
7 fused and 9–10 partially fused, and proximal palpal segment not swollen.

Male.—Habitus (Fig. 1); total length 0.6 mm; body black. *Head*: Eyes pubescent, dorsomedial separation of ommatidia not visible. Antennal flagellum (Fig. 2) with 11 flagellomeres, flagellomeres 2–7 fused, distal flagellomeres more elongate with 9 and 10 partially fused, flagellomere 11 distinctly shorter than fused 9+10; sensilla coeloconica not visible on flagellomere 1; flagellum length 340 μ m. Proboscis very short. Palpus (Fig. 3) with 2 segments; proximal segment large, possibly composed of fused segments 1–4, sensory pit not visible, palpal ratio ca. 2.30; distal segment (primitive 5th) short, bearing 3 terminal setae. *Thorax*: Legs with femora and tibiae slender; fore tibia (Fig. 4) lacking apical spur, hind tibia (Fig. 5) with small apical spur; hind tibial comb (Fig. 5) composed of 5 setae, 1st twice as long as others; hind tarsomere 1 (Fig. 5) with setae that are not of typical palisade configuration; hind tarsal ratio 2.64; tarsomere 4 of each leg (Figs. 4–5) elongate cylindrical, nearly as long as tarsomere 3 with apical recurved setae; tarsomere 5 of each leg (Figs. 4–5) slender, bearing minute, simple, equal sized claws. Wing (Fig. 6) length 0.50 mm; costal ratio 0.33; membrane covered with

coarse macrotrichia; only R, C and proximal portion of M well developed (Figs. 6–7), distal portions of M and CU and anal veins barely discernable; radial cells obsolete (Fig. 7), juncture of C+R darkly pigmented, forming a small stigma. *Abdomen*: Genitalia (Fig. 8) barely visible. Gonocoxite nearly straight; gonostylus long, slender, apex pointed. Tergite 9 with large distinct cerci; apicolateral processes not discernable.

Female.—Partially damaged during preparation of amber. Antennal flagellum (Fig. 9) with proximal 3 flagellomeres nearly globose, remaining flagellomeres gradually increasing in length; flagellomere 1 with at least 1 apical sensilla coeloconica; flagellum length 268 μ m; antennal ratio 0.86. Hind tibial comb (Fig. 10) with 5 setae, 1st distinctly longer than others; hind tarsomere 1 (Fig. 10) with setae forming a distinct row, hind tarsal ratio 2.42; hind tarsomere 4 (Fig. 10) cylindrical; hind tarsomere 5 (Fig. 10) swollen, bearing minute, simple, equal sized claws. Wing membrane (Fig. 11) covered with coarse macrotrichia; radial cells obsolete (observed before preparation).

Type material.—Holotype male, Dominican Republic, enclosed in Oligo-Miocene amber, specific provenance unknown, purchased in Santo Domingo by D. Grimaldi



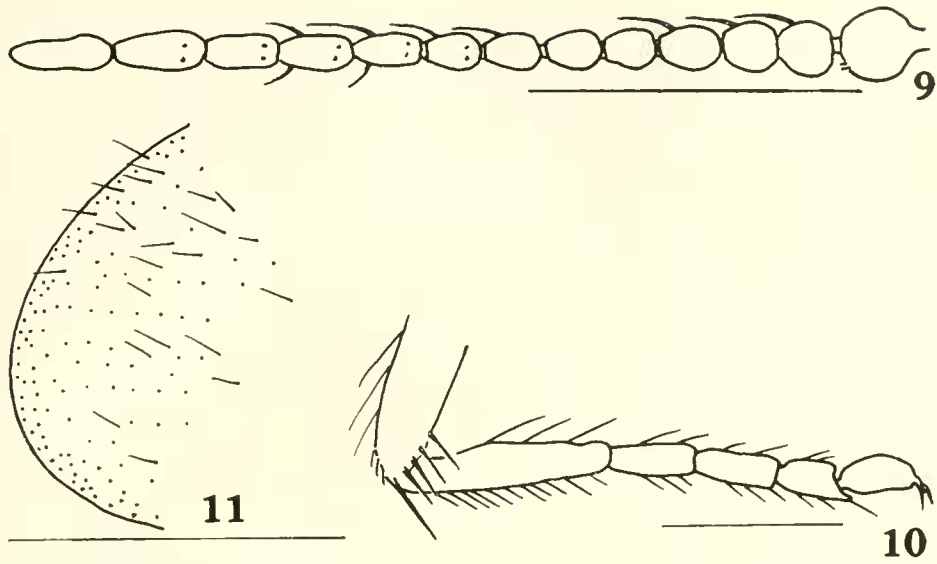
Figs. 1-8. *Baeodasyomyia dominicana*, male. 1, habitus; 2, flagellum; 3, palpus; 4, apex of tibia and tarsus of fore leg; 5, apex of tibia and tarsus of hind leg; 6, wing; 7, costa and radial veins of wing; 8, genitalia. Scales = 0.1 mm.

(AMNH, DR-8-112). Paratype female in amber with one beetle, Dominican Republic, Brodzinsky/Lopez-Penha amber collection (USNM #5540).

Etymology.—Named for the Dominican Republic, the country of origin of the amber on the island of Hispaniola (Fig. 16).

Discussion.—A male and female of the only other species in this genus, the extant *B. modesta* from Haiti and a male and fe-

male from Rio Raposo, Colombia (Fig. 16) differs from the new fossil species by the male which possesses an antenna (Fig. 14) with 10 flagellomeres, and a swollen proximal palpal segment. Clastrier and Raccurt (1979, Fig. 1A) illustrated the male antenna of *B. modesta* with 8 flagellomeres, but described it as having 10 flagellomeres. Clastrier (pers. comm.) informs us that this illustration is incorrect and that all of the



Figs. 9-11. *Baeodasymyia dominicana*, female. 9, flagellum; 10, apex of tibia and tarsus of hind leg; 11, apex of wing. Scales = 0.1 mm.

males in the type-series of *B. modesta* have 10 flagellomeres (Fig. 14). In addition, the hind tibial spur of *B. modesta* is more robust and bifid or trifid, whereas in *B. dominicana* it appears to be slender and entire. Finally, Table 3 presents some numerical characters for both of these species. Note that there is considerable overlap for most of these characters, and in those characters which do not overlap, the differences are minor.

Clastrier and Raccurt (1979) indicated that the wing veins of *B. modesta*, posterior to the r-m crossvein, were not evident. However, in their Fig. 1G, these veins are indicated by the presence of linear tracts of macrotrichia on the membrane. Our ex-

amination of this species reveals that the distal portions of the media, as well as the cubitus and anal veins, are in fact present but poorly marked. By carefully tracing the positions of the macrotrichia (or their sockets if the setae are broken off), a more or less dark line is evident, that reveals the true location of each vein.

The remarkable similarity of this fossil species to the extant species is an indication that evolution in this genus has been very conservative. DeSalle et al. (1992) reported only a 3% substitution of base pairs of the 16s rDNA between the extinct termite *Mastotermes electrodominicus* from Dominican amber and it's only extant relative, *M. dar-*

Table 3. Numerical characters of *Baeodasymyia modesta* and *B. dominicana*.

	<i>B. modesta</i>		<i>B. dominicana</i>	
	♂	♀	♂	♀
1. Wing length (mm)	0.44-0.48	0.40-0.47	0.50	—
2. Costal ratio	0.29-0.34	0.29-0.34	0.33	—
3. Antennal ratio	—	0.78-0.97	—	0.86
4. Flagellum length (µm)	344-362	287-300	340	268
5. Hind tarsal ratio	2.38-2.92	2.77-2.86	2.64	2.44
6. Palpal ratio	2.50-2.57	1.95-2.22	2.30	—

winiensis from Australia. Cano et al. (1992) reported a 7% substitution of base pairs of the 18s rRNA between the extinct stingless bee *Proplebeia dominicana* from Dominican amber, and two related extant species of the genus *Plebeia* from Central America. It is interesting to note that stingless bees and primitive termites like *Mastotermes* are both extinct in the Caribbean.

Phylogenetic Considerations.—When Grogan and Wirth (1980) proposed the genus *Nannohelea*, they suggested that it and *Baeohelea* Wirth and Blanton (1970) were sister groups, based on the fact that males in both genera possessed a reduced antennal flagellum. Although this seemed a reasonable assumption then, it was unfortunate that Clastrier and Raccurt's paper describing the new genus *Baeodasyomyia*, appeared too late (1979) for it to be considered in the paper on *Nannohelea* by Grogan and Wirth (1980).

Recently, Borkent (1992) presented evidence indicating that *Nannohelea* belongs to an assemblage of genera that possess at least one enlarged katapisternal seta. Grogan and Borkent (1992) proposed the new genus *Sinhalohelea* from Sri Lanka, which also has enlarged katapisternal setae, and indicated that it forms the sister group of *Brachypogon* + *Ceratoculicoides* + *Nannohelea* + *Rhynchohelea*.

Despite the fact that males of *Baeodasyomyia*, *Baeohelea*, *Nannohelea*, and some species of *Brachypogon* have a reduced antennal flagellum, this cannot be taken as evidence of their monophyly. In *Brachypogon* and *Ceratoculicoides*, flagellomere 11 is fused with the preceding proximal flagellomeres, a pattern not present in other ceratopogonid genera (Grogan and Borkent 1992). In *Baeodasyomyia* and *Baeohelea*, the distal three to four flagellomeres (primitive 9–13) are never fused with the preceding proximal flagellomeres. Furthermore, since *Baeodasyomyia* and *Baeohelea* lack katapisternal setae, they obviously cannot belong to the above assemblage of genera that possess this character.

Clastrier and Raccurt (1979) proposed *Baeodasyomyia* due to its resemblance to *Baeohelea*, and *Paradasyhelea* Macfie, a genus presently assigned to the tribe Culicoidini. Until a study in progress by Borkent on the phylogenetic relationships of all genera in the family is completed, we follow Wirth and Grogan (1988), and consider *Baeohelea* and *Baeodasyomyia* members of the tribe Ceratopogonini. The following characters provide evidence that these two genera form a monophyletic group, and are among the most highly modified and reduced genera in the tribe Ceratopogonini.

1. Palpus with three or more segments (plesiomorphic); palpus with two segments (apomorphic).

Baeohelea and *Baeodasyomyia* key to couplet 8 in the key to genera of Ceratopogonini in Wirth and Grogan (1988) by virtue of the fact that they are the only two genera in that tribe (and family) in which the palpus is reduced to only two segments. We consider this character to be a synapomorphy shared by both genera, and they are therefore sister groups, forming a monophyletic group.

The reduction of palpal segments in other genera with only one segment distal to the one bearing a sensory pit (primitive 3rd) has previously been explained as the result of the fusion of the 4th and 5th segments (Fig. 12A). However, an alternative explanation for the reduction and fusion of palpal segments is possible. We have examined a female of *Culicoides minutissimus* (Zetterstedt) from Poland in which the 4th palpal segment is fused with the 3rd (Fig. 12B). This specimen demonstrates that such a teratological fusion is possible, and likely explains the condition for genera such as *Baeodasyomyia* and *Baeohelea* in which the last palpal segment is small and the one bearing the sensory pit is enlarged.

2. Parameres of male genitalia present (plesiomorphic); parameres absent (apomorphic).

The parameres of the male genitalia in *Baeodasyomyia* and *Baeohelea* appear to have been lost and this may also be indic-

ative of their shared ancestry. This character state may be somewhat subject to homoplasy as parameres are reported to be absent in two other genera of Ceratopogonini. One of these, the Neotropical monotypic *Fittkauhelea* (Wirth and Blanton 1970), clearly belongs to another assemblage of genera including *Parabezzia*, *Diaphanobezzia* and *Heteroceratopogon* (Wirth and Grogan 1988). In the second genus, the poorly known Oriental *Campopterohelea* of unknown affinities, only the male of one of the five species is known, *C. distincta*, which was described by Dasgupta and Sarkar (1982) as lacking parameres.

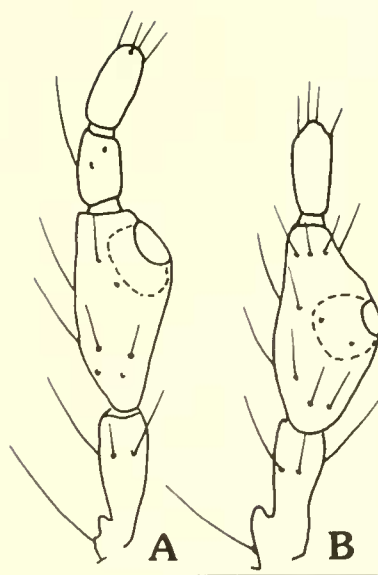
In addition, the vestigial mandible present in females of both genera may also be indicative of their shared ancestry. However, this character is subject to homoplasy as females with vestigial mandibles are found in at least one other genus in the tribe Ceratopogonini, *Notiohelea* (Grogan and Wirth 1979, Spinelli and Grogan 1990), as well as *Paradasyhelea* (tribe Cuclicoidini). There are other genera of ceratopogonids with species in which the female mandible is vestigial, such as in some autogenous species of *Culicoides* and in at least one species of the predaceous genus *Serromyia* (Borkent and Bissett 1990). However, this condition is rare and clearly not universal for the majority of species in these genera.

3. Fore tibial spur present (plesiomorphic); spur absent (apomorphic).

The fore tibia of *Baeodasymyia* lacks an apical spur, a character present in all other genera of ceratopogonids. Therefore, we interpret the loss of the fore tibial spur as an autapomorphy in *Baeodasymyia*, and evidence of its recognition as a monophyletic group.

4. Male antenna with 7 or more flagellomeres (plesiomorphic); with 6 flagellomeres (apomorphic).

In males of *Baeohelea*, the distal three elongated flagellomeres contain only a single row of sensilla chaetica (Fig. 15), a pattern different from that of *Baeodasymyia*. Examination of a male of *Baeohelea* reveals

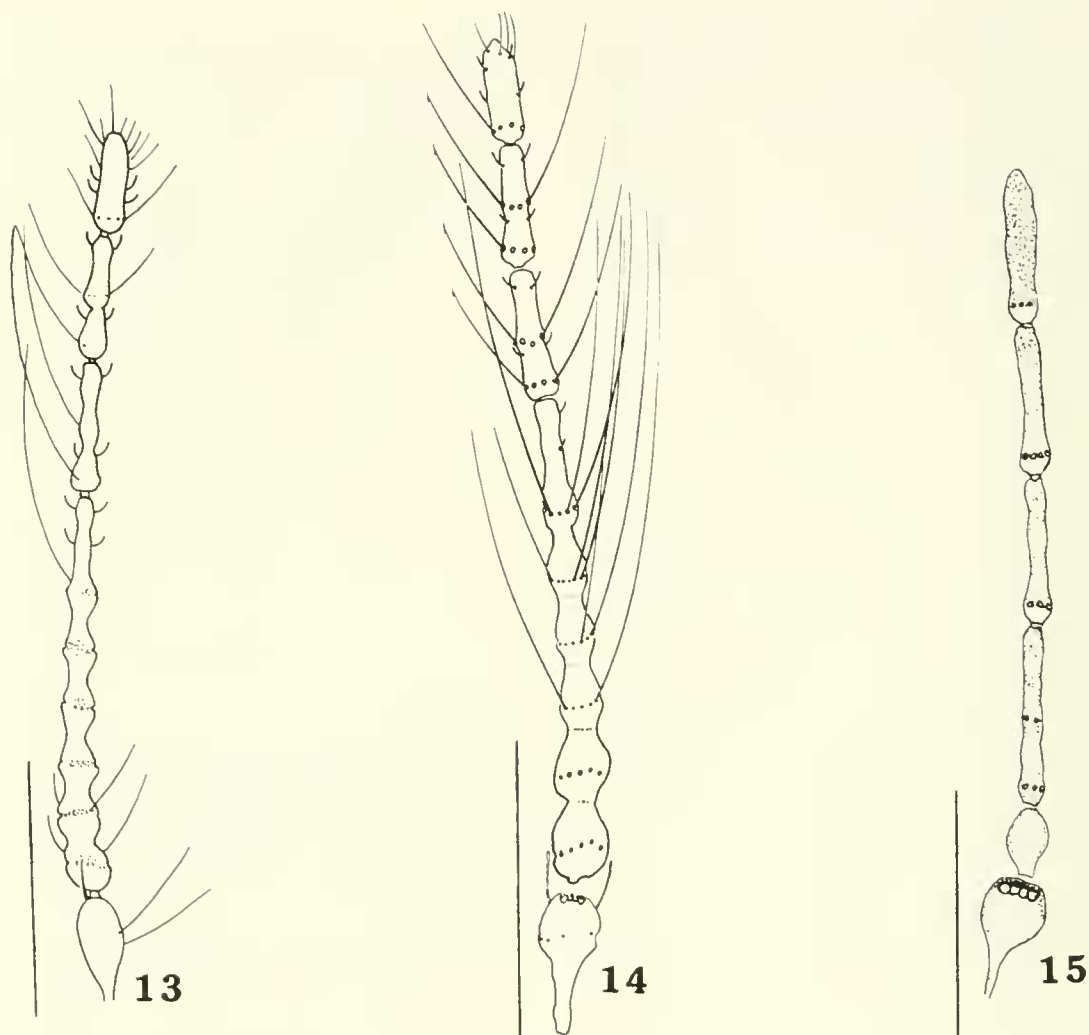


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Fig. 12. *Culicoides minutissimus*, female. A, normal palpus; B, palpus with fused 3rd and 4th segments. Scale = 0.1 mm.

that the first of its elongated distal flagellomeres (flagellomere 3), contains two to four partial or complete rows of sensilla chaetica. This indicates that this flagellomere represents the fusion of at least two or more proximal flagellomeres and that the pattern of fused flagellomeres in *Baeohelea* may be the result of a different genetic mechanism than in *Baeodasymyia* or *Nannohelea*. Furthermore, *Baeohelea* is the only genus of ceratopogonids in which the male has only six flagellomeres, and the only genus with less than 10 flagellomeres in which the distal four are elongated. The males of three species of *Nannohelea* have only seven flagellomeres, but the number of elongated distal flagellomeres is either two (*N. fuscipennis*) or three (*N. clastrieri* and *N. tamil*) (Grogan and Wirth 1980, 1990). We interpret this fusion pattern and reduction to only six flagellomeres in the male as an autapomorphy unique to *Baeohelea* and evidence of its monophyly.

Grogan and Borkent (1992) noted in males of *Nannohelea* that some of their distal fla-



Figs. 13–15. Male antennal flagella of: 13, *Baeodasymyia dominicana*; 14, *B. modesta* (modified after Clastrier and Raccurt); 15, *Baeohelea nana* (modified after Wirth and Blanton). Scales = 0.1 mm.

gellomeres contained a double row of setae (sensilla chaetica). They interpreted this as evidence that these flagellomeres were formed as the result of fusion of two or more primitive flagellomeres. Examination of males of *Baeodasymyia modesta* reveals that the penultimate two flagellomeres contain a double row of sensilla chaetica and represents the results of the fusion of the primitive 9+10 and 11+12 (Fig. 14). This fusion is only partially completed for flagellomeres

9 and 10 (primitive 11 and 12) in the fossil *B. dominicana* (Fig. 13).

Bionomics and distribution.—*Baeodasymyia modesta* is known from Colombia (Wirth and Grogan 1988) and Haiti (Fig. 16) where adults were reared from the sandy edges of rivers (Clastrier and Raccurt 1979).

Baeohelea nana is known from Colombia, Dominica and Ecuador (Fig. 16), and in Dominica is confined to the rainforest at or above 2000 ft (Wirth and Blanton 1970).

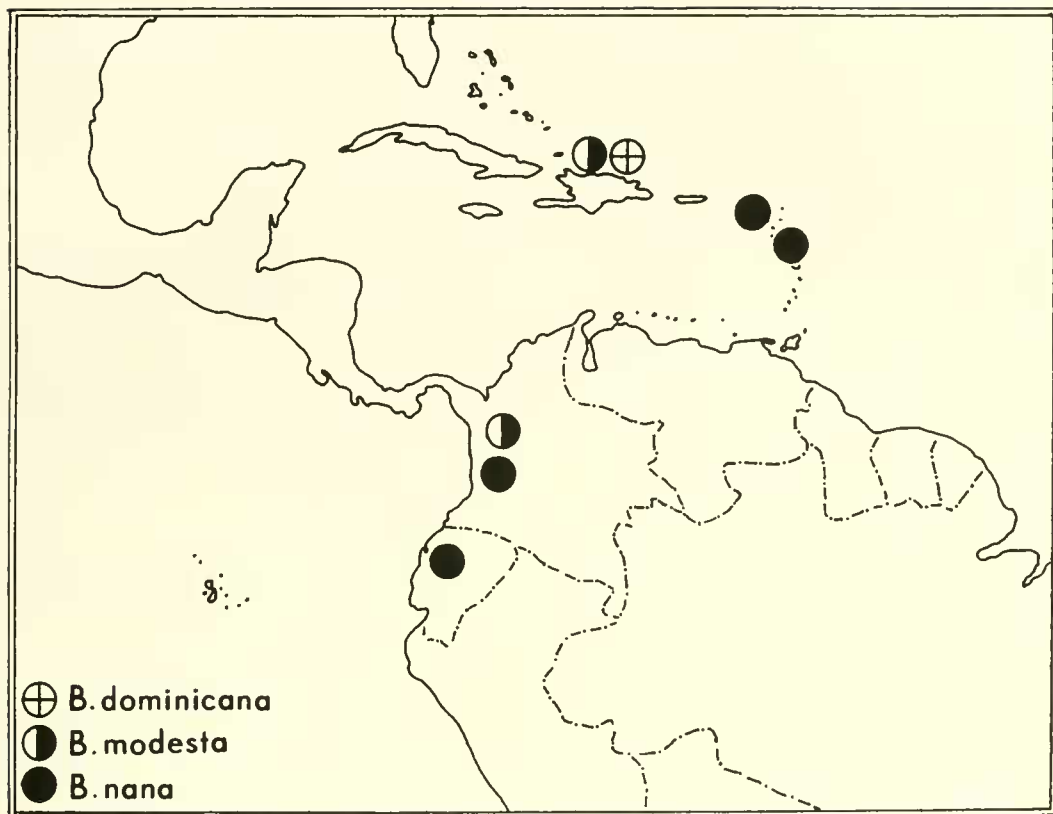


Fig. 16. Locality records for *Bacodasymyia dominicana*, *B. modesta*, and *Bacodasymyia nana*.

Borkent (pers. comm.) collected this species on St. Kitts from a wet rainforest near a small waterfall 1.6 km N of Basseterre on 11 November 1985 at 443 m, and represent the first record of this species from that island (Fig. 16).

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